Overlooked flower-visiting Orthoptera in Southeast Asia

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Abstract

The study of insect–plant interactions such as flower visitors, pollinators, and florivores, are important for understanding the natural world. However, not all flower-visiting insects are equally well known, especially in the biodiverse Southeast Asian region. One group is the orthopterans, comprising of grasshoppers, crickets, and katydids. Natural history observations were made around Southeast Asia to document flower-visiting orthopterans. Owing to the limited studies on the ecology of orthopterans in Southeast Asia, we provide here the first documentation of flower-visiting orthopterans from Southeast Asia and the most extensive one for the Tropics. Based on 140 incidences of orthopteran visiting flowers, 41 orthopteran species have so far been recorded to visit 35 different plant species, in mainly Singapore, Malaysia, part of Thailand, and Brunei Darussalam. We conclude that orthopterans are indeed overlooked flower-visitors in this region and warrant further investigation.

Key words

florivory, insect-plant interaction, natural history, pollination

Introduction

Insects and plants make up a large proportion of the organismal diversity on Earth. Interactions between plants and insects are complex and can be intriguing (Novotny et al. 2006, Hu et al. 2008, Lewinsohn and Roslin 2008, Novotny and Miller 2014). Research on insect–plant interactions helps to shape our understanding of ecology and coevolution (e.g. Crepet 1984, Grimaldi 1999, Novotny et al. 2006, Novotny and Miller 2014), resource management (e.g. Lundberg and Moberg 2003, Cardel and Koptur 2010, Hudewenz et al. 2012), and conservation (e.g. Kearns et al. 1998, Bale et al. 2002, Tscharntke and Brandl 2004). There are many aspects to insect–plant interactions, such as pollination biology and herbivory (and more specifically, folivory). Among the different functional groups of flower-visiting insects, a less-studied group is the florivores (as compared to pollinators) (Breadmore and Kirk 1998, McCall and Irwin 2006). Florivory is defined as the feeding of floral parts, and florivores can have direct and indirect effects on floral adaptions, interspecific interactions, and community dynamics (e.g. Krupnick and Weis 1999, Krupnick et al. 1999, Frame 2003, McCall and Irwin 2006). While we have estimates for flower pollinator-insect species (Bawa et al. 1985, Ollerton et al. 2011) and for folivore-insect species (Ødegaard 2000, Novotny et al. 2006, Dyer et al. 2007), we do not have a good estimate of the number of insect species that feed on flowers (Wardhaugh 2015).

Many insects visit flowers, and some primarily feed on flowers (Rentz and Clyne 1983, Rentz 1993, Rentz 2010, Corlett 2016, Kondo et al. 2016, Sing et al. 2016). These include members of the Coleoptera, Blattodea, Hemiptera, and Orthoptera (Nagamitsu and Inoue 1997, Wardhaugh 2015). The Orthoptera is an order of insects commonly known as the grasshoppers, crickets, and katydids. There are more than 27,000 species globally, and about 2,000 recorded species in biodiverse Southeast Asia (Myers et al. 2000, Cigliano et al. 2017, Tan et al. 2017a). Owing to the diversity in species and forms, orthopterans provide numerous ecosystem functions, such as herbivory (including florivory) (Tan and Tan 2017, Tan et al. 2017b), predation (Poo et al. 2016), and even pollination (Hugel et al. 2010, Micheneau et al. 2010, Lord et al. 2013). Nonetheless, few records of orthopterans visiting flowers have been published (see e.g. Schuster 1974, Rentz and Clyne 1983, Micheneau et al. 2010, Rentz 2010, Wardhaugh 2015, Krenn et al. 2016) and none of these involve Southeast Asian orthopterans. This is not surprising since even studies on the taxonomy of orthopterans in Southeast Asia remain incomplete and fragmentary (Tan et al. 2017a).

Understanding the diversity of flower-visiting orthopterans can have potential applications. As many Southeast Asian coun-

tries still rely on agriculture as a main source of economic growth (Rigg 1998), baseline information on flower-visitors may be useful to managers to take notice of potential orthopteran pests in the future (Jago 1998, Willemse 200l, Alford 2012). Nevertheless, orthopterans may also potentially be pollinators of flowers they visit (Micheneau et al. 2010), hence providing a valuable service to plants. Without such documentation, it is not possible to assess the risks presented by these potential pest species, as well as to conduct further investigations into the beneficial roles of the flower-visiting orthopterans.

Here, we surveyed seven localities around Southeast Asia and made natural history observations of orthopterans visiting flowers. We identified the orthopteran and plant species, whenever possible, and provided notes and remarks on the behaviour and ecology. We aim to provide the first report of flower-visiting orthopterans in this region and provide baseline information for further investigation into flower-visiting, florivory and pollination by orthopterans.

Material and methods

Field observations.—Natural history observations were carried out between 2015–2017 mainly in seven surveyed sites around Southeast Asia (Fig. 1, Table 1). A few sporadic observations were also made from four other locations in Southeast Asia by chance (Fig. 1). Opportunistic observations were made during both day and night because many flower-visiting orthopterans are nocturnal, while some are more active in the day. We considered an orthopteran a flower-visitor if it i) exhibited foraging or feeding behaviours and ii) carried pollen grains. This reduced overestimation owing to orthopterans landing on flowers by chance. The orthopterans and flowers were identified in the field with the aid of guides (e.g. Tan 2012a, 2012b, Tan and Kamaruddin 2014, Dawwrueng et al. 2017), whenever possible. Otherwise, specimens were collected for further identification. Whenever possible, photographs were taken using a Canon EOS 500D digital SLR camera with a compact-macro lens EF 100 mm 1:2.8 USM. The specimen's life stage and presence of pollen grains were noted, and the GPS coordinates of the locality were recorded.

Analyses.—To visualise and summarise the respective orthopteran species that visited a specific flower species, an interaction network was constructed using the 'plotweb' function in bipartite package (Dormann et al. 2008) in R software v.3.3.3 (R Core Team 2016). The default method "cca" was used to minimise the number of crossings between the orthopteran and plant levels.

Results

Observations.—We recorded 140 incidences of orthopterans visiting flowers in five countries around Southeast Asia: Singapore (82), Peninsular Malaysia (23), Thailand (27), Brunei Darussalam (7), and Indonesia (1). While the sampling was distinctly higher in Singapore, the species that were recorded are mostly Southeast Asian species and can be found in most parts of Southeast Asia.

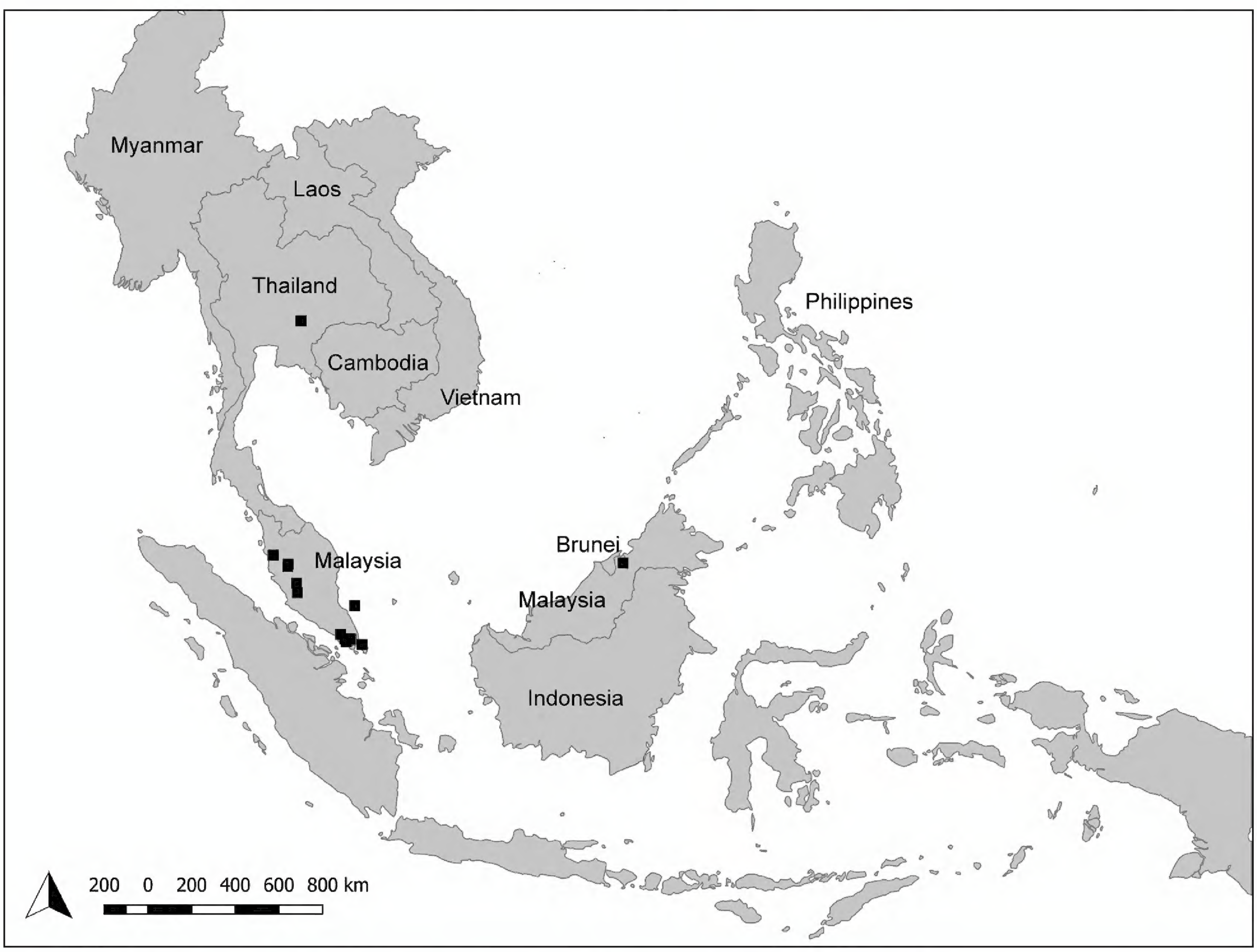

Fig. 1. Map of Southeast Asia with black squares indicating sampling locations between 2015–2017.

Table 1. A list of localities and habitats surveyed between 2015–2017.

No.	Locality	Habitat(s) Surveyed	Sampling effort (in days)
1	Singapore	Scrublands, gardens, herbaceous plots, lowland secondary forests	>100
2	Bukit Larut, Perak, Peninsular Malaysia	Gardens, lowland secondary forests, herbaceous plots, lower montane forests	12
3	Bukit Fraser, Pahang, Peninsular Malaysia	Gardens, lower montane forests	27
4	Ulu Gombak Field Studies Centre, Selangor, Peninsular Malaysia	Lowland secondary forests	4
5	Pulau Tioman, Pahang, Peninsular Malaysia	Gardens, lowland secondary forests	3
6	Sakaerat Biosphere Reserve, Nakhon Ratchasima, Thailand	Dry dipterocarp forest, dry evergreen forest, herbaceous plots	36
7	Kuala Belalong Field Studies Centre, Temburong, Brunei Darussalam	Gardens, primary hill dipterocarp forests	21

Habitats with the largest number of observations include scrublands (59), and evergreen dipterocarp forest and gardens (both 13). In total, 99 records were of Ensifera (crickets and katydids) in contrast to 41 of Caelifera (grasshoppers). Fifty of the orthopteran records were adults whereas 90 were nymphs.

Species richness.—Forty-one orthopteran species from six families were recorded to visit flowers of 35 plant species from 15 families (Fig. 2). The coverage of flower-visiting orthopteran lineages in the orthopteran phylogeny was restricted to five main clades among the 10 lineages (Song et al. 2015): (i) Grylloidea, (ii) Tettigonioidea, (iii) Pyrgomorphoidea, (iv) Acridoidea, and (v) Stenopelmatoidea.

Network.—We found that most flower-visiting orthopterans visit very few flower species (Fig. 2). Only *Phaneroptera brevis* (Serville, 1838) (13), *Nisitrus vittatus* (Haan, 1844) (8), *Valanga nigricornis* (Burmeister, 1838) (6), *Conocephalus* species (5), *Xenocatantops humilis* (Serville, 1838) (5), and *Atractomorpha* species (4) visited more than three different flower species (Fig. 3). Most flower-visiting orthopterans are also widely distributed species across Southeast Asia or parts of Southeast Asia (except *Tremellia timah* Gorochov and Tan, 2012 which is so far known only from Singapore). Likewise, many flowers were visited by only a few orthopteran species (Fig. 2). *Ageratum conyzoides* L. (7), *Bidens pilosa* L. (7), *Praxelis clematidea* (Griseb.) (15), and *Sphagneticola trilobata* (L.) (6) (all Asteraceae), and *Lantana camara* L. (Verbenaceae) (6) were among the most widely visited flowers. Only 19% (26 observations) of total observations had the respective orthopteran carrying some pollen grains on its body.

Discussion

Orthopterans are only some of the many invertebrates that visit flowers (Wardhaugh 2015). To our best understanding, we provide here the first documentation of flower-visiting orthopterans from Southeast Asia and the most extensive one from the tropical region. The last known report by Schuster (1974) listed merely seven orthopteran species visiting six flowers from Peru and Panama from two years of sampling which may also have underestimated the diversity of flower-visiting orthopterans. Wardhaugh (2015) suggested that orthopterans are rare flower-visitors but we showed that there are more flower-visiting species than previously known.

There are two main types of orthopterans that visit flowers. Firstly, some orthopterans are floriphilic, clearly preferring flowers over other plant parts as their diet (Tan and Tan 2017). These include species from the subfamily Phaneropterinae (katydids) (Rentz 2010, Suetsugu and Tanaka 2014). Some of these katydids even specialize on flowers (Rentz 2010, Hemp et al. 2013). These floriphilic species also tend to feed more on the pollen and nectar of the flowers (Rentz and Clyne 1983, Suetsugu and Tanaka 2014). In Southeast Asia, *P. brevis* is a very common scrubland species and has been observed frequently visiting the flowers of different species. Juveniles of Phaneropterinae are also often encountered visiting flowers along forest edges in different parts of Southeast Asia (Fig. 4). Orthopterans from the subfamilies Zaprochilinae and Phasmodinae are known as specialist flower-feeders (Rentz 1993) but they are endemic to Australia. Apart from a raspy cricket from the Mascarene Islands acting as an obligate pollinator of an orchid (Micheneau et al. 2010), we have not established any obligate specialist flower-visiting orthopterans from Southeast Asia based on our sampling.

The second group of flower-visiting orthopterans are opportunistic polyphagous species. These polyphagous species are usually folivores (feeding on the foliage) but can be facultative florivores when floral parts are available (Burgess 1991, Bernays and Chapman 2007, Higginson et al. 2015). They were observed to feed on the petals and/or petal-like analogues (e.g. ray florets of a capitulum and flag calyx lobes). Examples of these species are *V. nigricornis* (Fig. 3c) and *X. humilis* (Fig. 3e) which are also known to be economic pests around Southeast Asia (Willemse 2001). By feeding on flowers, these facultative florivores can obtain supplementary nutrition (Held and Potter 2004, Merwin and Parrella 2014) since floral parts tend to (but not always) contain greater concentrations of nitrogen and water while not being as tough as leaves (e.g. Thompson 1983, Burgess 1991).

Nonetheless, there are also other interesting encounters of flower-visiting orthopterans. These include a predatory katydid from the subfamily Meconematinae feeding on flowers of *Dillenia suffruticosa* (Griff. ex Hook.f. and Thomson) (Fig. 5a). It is unclear exactly why a predatory katydid would visit flowers, but we suspect that it is eating the pollen in the anthers of the smaller stamens at the base of the whorl of larger stamens. This species may be exploiting a cheap source of protein since adinandra belukar (a species-poor, anthropogenic heath forest dominated by *Adinandra dumosa* Jack [Sim et al. 1992]) tends to be more faunistically depauperate because of the poorer soils in this forest type (Sim et al. 1992, Chua et al. 2013, 2016).

We observed that non-native weeds in Southeast Asia are frequently visited by many orthopterans. These weeds tend to flower

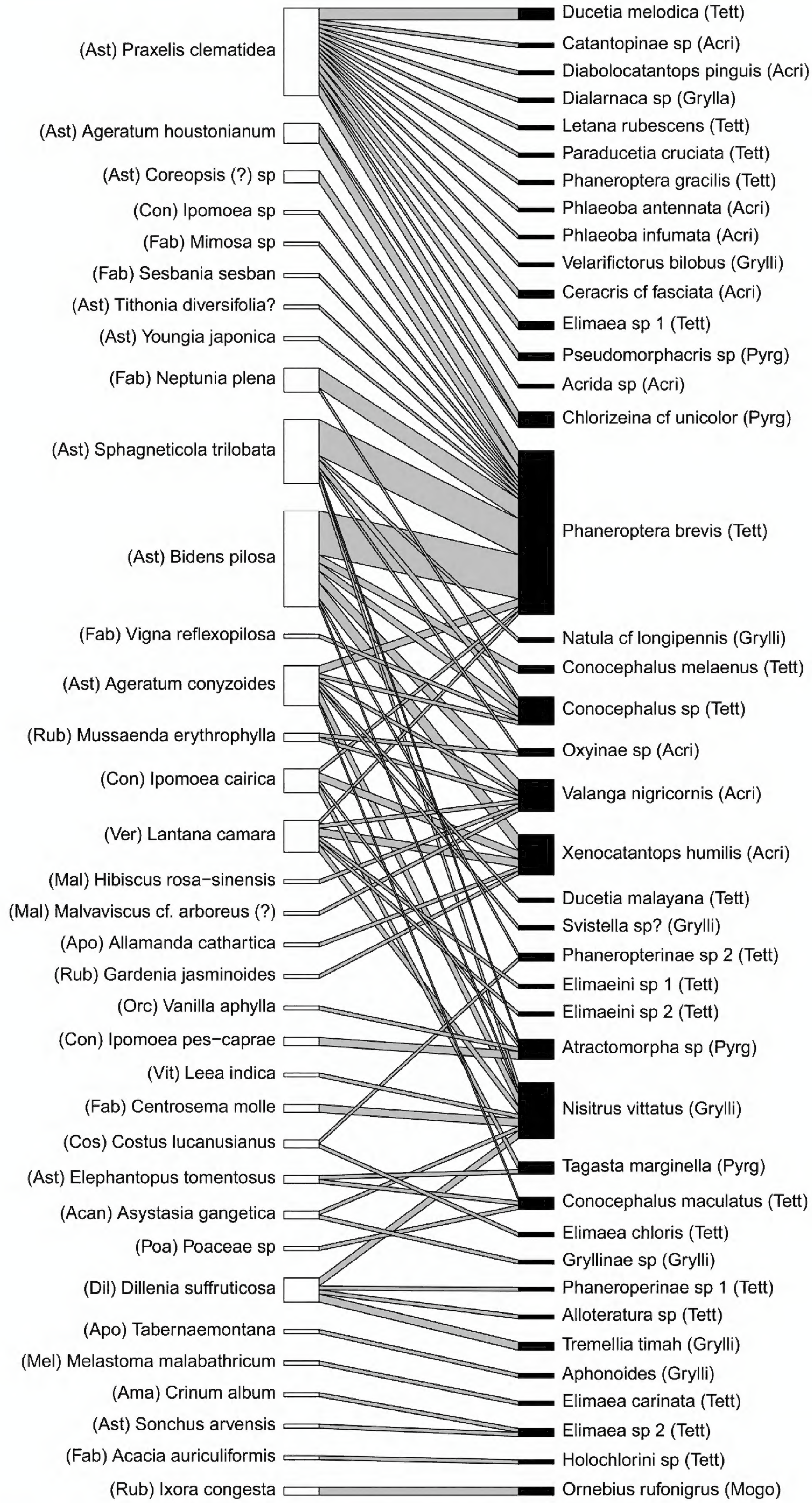

Fig. 2. The interaction web between flower-visiting orthopterans (right row) and flower species (left row) in Southeast Asia. The width of the linkage represents the number of observations. Legends for orthopteran families: Acri = Acrididae; Grylla = Gryllacrididae; Grylli = Gryllidae; Mogo = Mogoplistidae; Pyrg =Pyrgomorphidae; Tett = Tettigoniidae. Legends for flower families: Aca = Acanthaceae; Ama = Amaryllidaceae; Apo = Apocynaceae; Ast = Asteraceae; Con = Convolvulaceae; Cos = Costaceae; Dil = Dilleniaceae; Fab = Fabaceae; Mal = Malvaceae; Mel = Melastomataceae; Orc = Orchidaceae; Poa = Poaceae; Rub = Rubiaceae; Ver = Verbenaceae; Vit = Vitaceae.

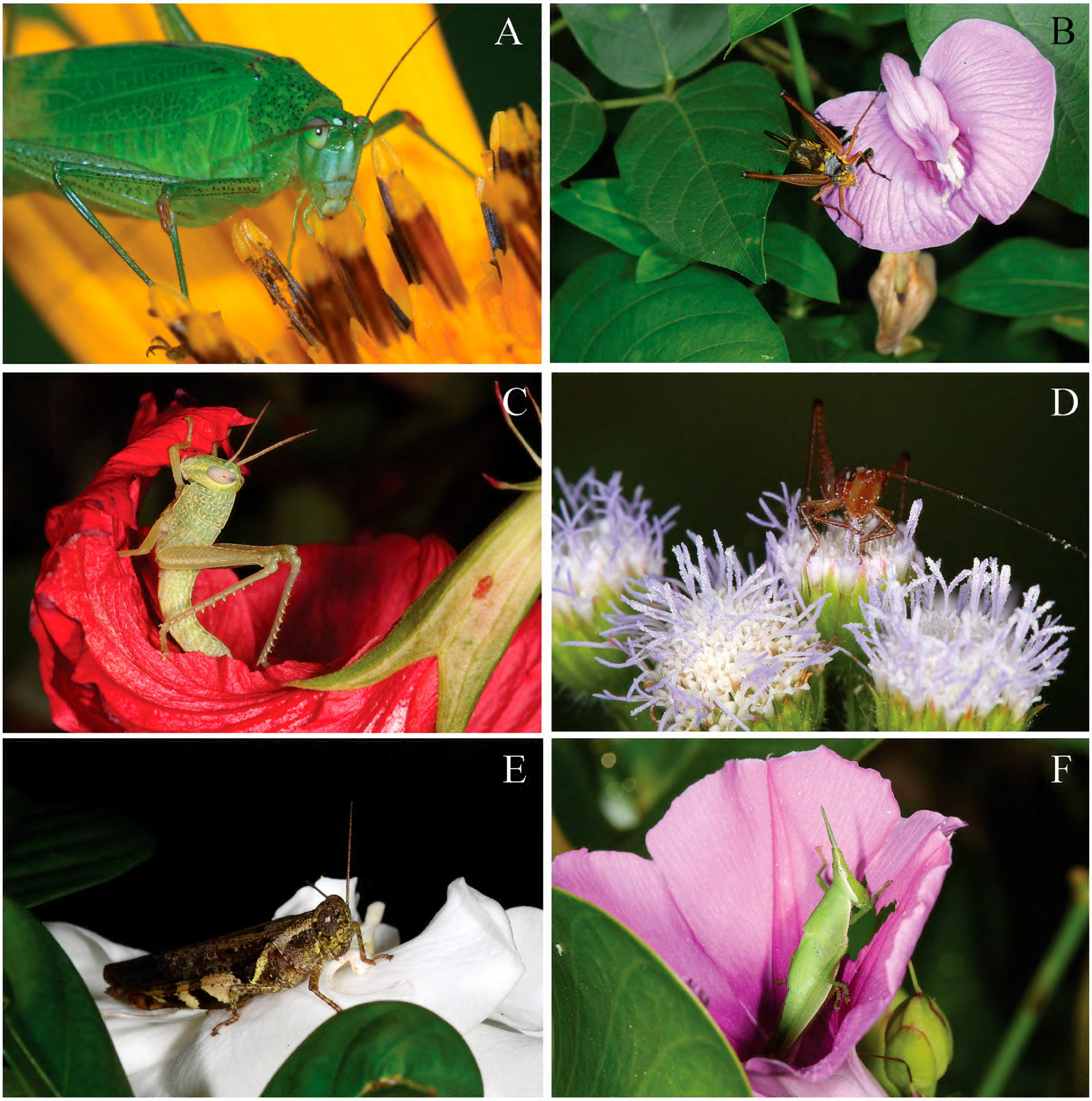

Fig. 3. Examples of common flower-visiting orthopterans from Southeast Asia: **A.** *Phaneroptera brevis* feeding on the anthers of *Tithonia diversifolia* in Bukit Larut, **B.** *Nisitrus* species feeding on the petals of *Centrosema molle* in Ulu Temburong, **C.** *Valanga nigricornis* feeding on a corolla lobe of *Hibiscus rosa-sinensis* in Pulau Tioman, **D.** *Conocephalus* species feeding on the florets of *Ageratum conyzoides*, **E.** *Xenocatantops humilis* feeding on a corolla lobe of *Gardenia jasminoides* in Singapore, and **F.** *Atractomorpha* species on the corolla of *Ipomoea pes-caprae* in Pulau Tioman.

frequently and abundantly. In scrublands in Singapore, *B. pilosa* is a prominent weed and is known to be an important food source for many flower-visitors including the pollinator bees (Lok et al. 2010, Tan et al. 2017b). In the more exposed patches of the dry deciduous and evergreen dipterocarp forests in Sakaerat, many orthopterans were found to feed on weedy *P. clematidea* (Fig. 6). These include floriphilic katydids (e.g. *Ducetia melodica* Heller and Ingrisch, 2017, *Paraducetia cruciata* (Brunner von Wattenwyl, 1891), and *Letana rubescens* (Stål, 1861)) and opportunistic species (e.g. *Dialarnaca*? species and *Velarifictorus* (*Pseudocoiblemmus*) *bilobus* Tan et al., 2015).

Gardens, where different kinds of flowers (often of non-native species) are planted, are another habitat with numerous records of flower-visiting orthopterans. In the highlands of Peninsular Malaysia, gardens are common in hill resorts and the flowers tend to attract floriphilic orthopterans. Some of these flowering plants (e.g. *Ageratum houstonianum* Miller and *Tithonia diversifo-*

Fig. 4. Examples of unidentified Phaneropterinae nymphs visiting flowers of various plants: **A.** *Dillenia suffruticosa* in Singapore, **B.** *Acacia auriculiformis* in Singapore, **C.** *Costus lucanusianus* in Singapore, **D.** *Youngia japonica* in Bukit Larut, **E.** *Praxelis clematidea* in Sakaerat, and **F.** *Lantana camara* in Sakaerat.

lia (Hemsl.) (Fig. 3a) have become naturalised and can be found near the edges of pristine, lower-montane forests. Similarly, the high diversity of flower plants in gardens such as the Singapore Botanic Gardens can also attract floriphilic orthopterans (Fig. 3e). This corroborates findings of how flowers in gardens (particularly in urban areas) can generally help attract native insects including pollinators and orthopterans (Matteson and Langellotto 2011, Blaauw and Isaacs 2014, Garbuzov and Ratnieks 2014, Shwartz et al. 2014, Vrdoljak et al. 2016).

Native plant species that flower regularly are also visited by orthopterans. These include *D. suffruticosa* (Fig. 4a), *Melastoma malabathricum* L. (Fig. 5c), and *Ixora congesta* Roxb. (Fig. 5d), all from secondary forests, and beach vegetation species, *Ipomoea pes-caprae* (L.) (Fig. 3f). While many of the orthopterans that visit non-native plants are non-forest species, forest species such as *T. timah* (Fig. 5b) and *Ornebius rufonigrus* Ingrisch, 1987 (Fig. 5d) (both of which tend to be found in coastal forests in Singapore) do also visit flowering plants in secondary forests. We would

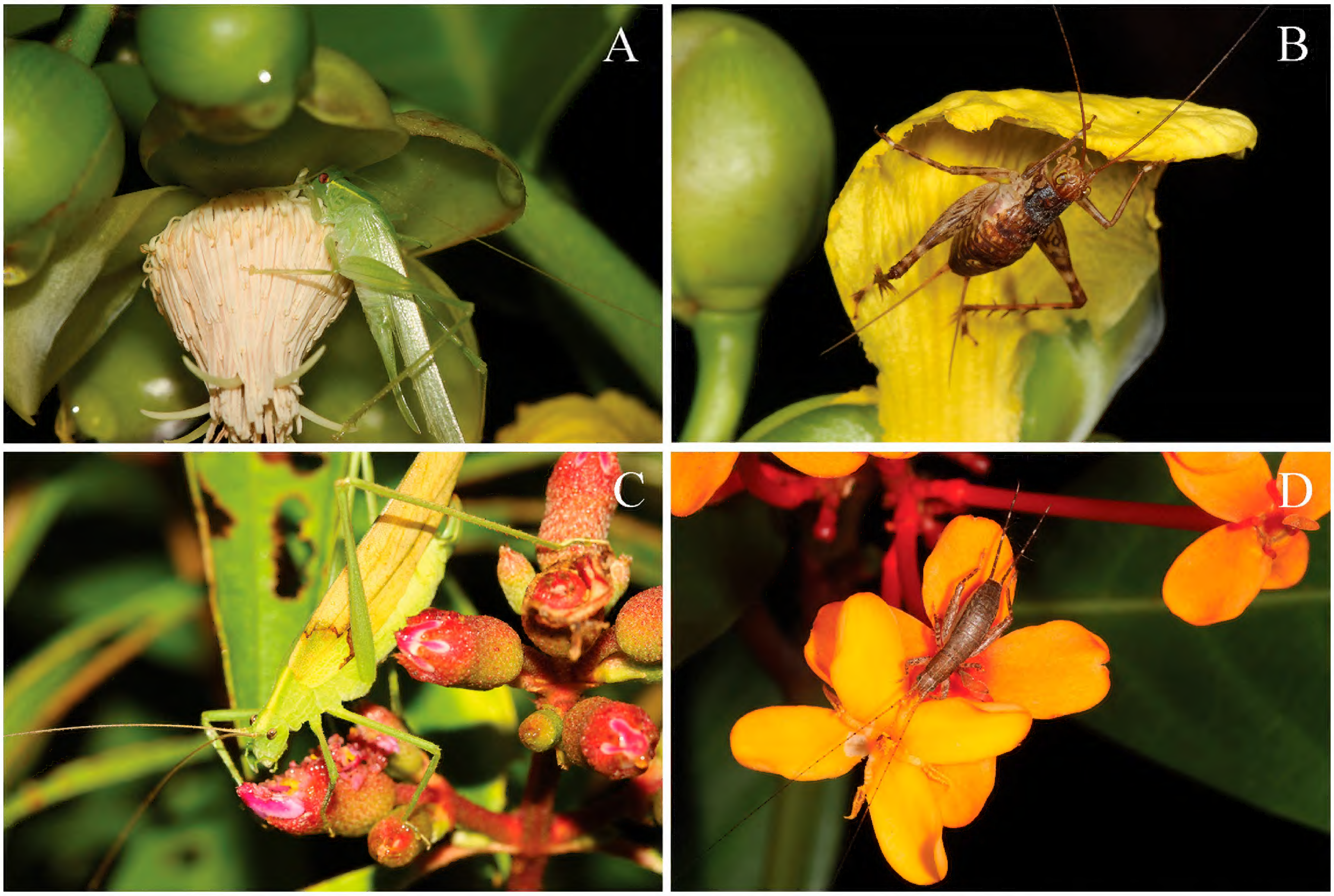

Fig. 5. Examples of flower-visiting orthopterans on native plant species: **A.** *Alloteratura* species on *Dillenia suffruticosa* in Singapore, **B.** *Tremellia timah* on *Dillenia suffruticosa* in Singapore, **C.** *Elimaea carinata* on *Melastoma malabathricum* in Singapore, and **D.** *Ornebius rufonigrus* on *Ixora congesta* in Singapore.

expect more forest orthopterans to visit flowers of dipterocarp forest species during synchronous flowering events (also called masting or mass flowering). Owing to the relatively rare synchronous flowering events (Jackson 1978, Chang-Yang et al. 2013, Lasky et al. 2016), we did not encounter any synchronous flowering events between 2015 and 2017 in the surveyed sites. As such, we were hitherto unable to document dipterocarp flower-visiting orthopterans.

While we provide baseline information of flower-visiting orthopterans in Southeast Asia, there is still a dearth of information on the ecology and behaviours of flower-visiting orthopterans from this region. A major area for further study is to monitor how flower-visiting orthopterans respond to synchronous flowering events in the dipterocarp forests (Bawa et al. 1985, Azmy et al. 2016). Studies on the relationship between insects and flowering phenology tend to focus on pollinators and their effects on the fruiting output of the flowering species, but we also know little about the effect of florivores (Gross and Werner 1983, Appanah 1985, Elzinga et al. 2007). Investigation into the latter can help us understand how plants respond to florivores and to make comparisons with herbivory escape via synchronous leaf production (Aide 1992, van Schaik et al. 1993, Reich 1995). Additionally, many forest orthopteran species are also cryptic and rare (yet diverse), and as such, we expect there may be many more flower-visiting orthopterans than what we have observed here, as well as perhaps novel behaviours or ecological patterns.

We should also aim to better understand the distribution of flower-visiting orthopterans as well as how to predict their occurrences. Although presence-only data can be challenging to analyse using conventional modelling techniques, recent development of MaxEnt modelling can help to overcome the shortcomings of such data (Jiménez-Valverde et al. 2008). In fact, MaxEnt modelling has been shown to be able to predict insect–plant distribution of suitable and non-suitable habitats for insect pests and hosts, thus assessing vulnerability to insect pests (e.g. Barredo et al. 2015, Restrepo Correa et al. 2016). However, we still need more observational records before running a robust and predictive MaxEnt model to understand the occurrence and distribution of flower-visiting orthopterans in this region (Pearse and Altermatt 2015). These can in turn address our knowledge gaps on the understudied ecological roles of orthopterans as florivores and/or pollinators, particularly in Southeast Asia.

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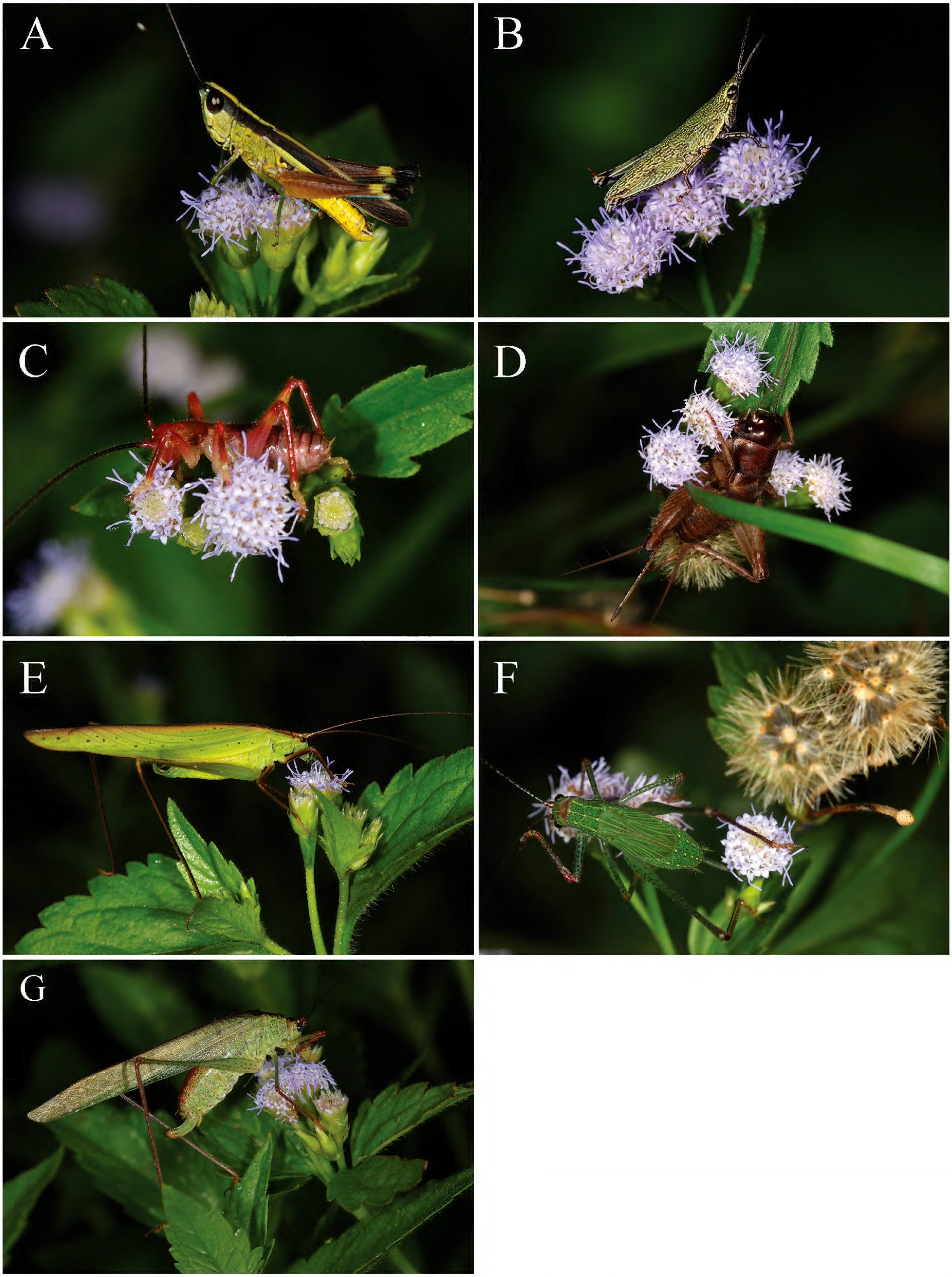

Fig. 6. Examples of flower-visiting orthopterans visiting weedy *Praxelis clematidea* in Sakaerat: **A.** *Ceracris* cf. *fasciata*, **B.** *Chlorizeina* cf. *unicolor*, **C.** *Dialarnaca*? species, **D.** *Velarifictorus* (*Pseudocoiblemmus*) *bilobus*, **E.** *Ducetia melodica*, **F.** *Paraducetia cruciata* and **G.** *Letana rubescens*.

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